

THE DISCOVERY OF A NOVEL BACTERIAL SPECIES IN THE GENUS  
*PAENIBACILLUS* FOUND IN GREAT SMOKY MOUNTAINS NATIONAL  
PARK

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## 1. ABSTRACT

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The All Taxa Biodiversity Inventory (ATBI) is an effort to record all species within Great Smoky Mountains National Park (GSMNP). When it was first begun nearly 20 years ago, prokaryotic organisms were not included as targets of the ATBI, but the project has been expanded to include prokaryotic organism and even viruses. The purpose of this study was to fully characterize and identify a unique bacterium cultured from soil from the Kephart Prong area of GSMNP as a novel species to science and for inclusion in the ATBI. Previous work showed that the isolate being studied aligned to the genus *Paenibacillus* based on 16S rDNA analyses but it was not closely related to any known species. The isolate was tested using various phenotypic measurements including colony characteristics, growth assessment under numerous conditions and many media formulations, in addition to cellular features observed using microscopy (e.g., Gram staining, flagella staining, endospore staining). Phylogenetic analysis of the entire 16S rDNA was undertaken and whole genome sequencing was performed to better differentiate the isolate from its closest relatives. The isolate is a Gram-positive, spore-forming rod that grows best at a pH from 7-9, NaCl concentration of 0-1%, and temperatures from 25-30°C. Transmission electron microscopy revealed cells that were rod shaped and 0.8µm in diameter x 2.8-3.2 µm in length, with flagella associated with the cells. The isolate was able to hydrolyze lipids, gelatin, casein, and starch in addition to having the ability to reduce nitrate to nitrite, and could utilize glucose via the butanediol fermentation pathway under anaerobic

conditions. The isolate was resistant to the antibiotic colistin, but susceptible to tetracycline, chloramphenicol, nitrofurantoin, nalidixic acid, penicillin, and clindamycin. The 16S rDNA sequence of the isolate most closely matched *Paenibacillus castaneae* with an 84.6% similarity. Analysis of the whole genome showed the closest match to *Paenibacillus harenae*, but major DNA sequence differences exist between the two species. With the information obtained from the 16S rDNA analyses, whole genome sequencing, and the growth-based tests, it appears that this isolate is likely a novel species within the genus *Paenibacillus*. This work represents the most complete account of a species of *Paenibacillus* to date in GSMNP. Phenotypic testing and whole genome sequencing results suggest that this organism can break down insect and fungi material via the use of chitinase genes, it can break down blood cells and utilize heme, and that it is resistant to colistin and, potentially tetracycline based on putative genes. Some genes found within the genome suggest that this species could have pathogenic capabilities. Outside of GSMNP, this research can aid in the understanding of other *Paenibacillus* species throughout the world that may not have been discovered yet by providing a template genomic sequence from a closely related species. Understanding of this novel species could also provide information on new ecological capabilities that may have not been established in previously discovered *Paenibacillus* species.

## 2. INTRODUCTION

Microorganisms are the oldest known life forms on Earth, dating back to about 3.9 billion years. The first microorganisms were believed to be anaerobic (living without oxygen) bacteria due to the Earth's anoxic atmosphere at the time. Over time, three domains of life emerged, the *Bacteria*, *Archaea*, and *Eukarya*. The three domains are split into two divisions: prokaryotes and eukaryotes; prokaryotes include *Bacteria* and *Archaea*, and eukaryotes comprise the domain *Eukarya*. The majority of species on Earth are prokaryotes and many others are eukaryotic microbes. Microorganisms can be found everywhere on Earth, such as in the soil, air, water, animals, and plants. Most are invisible to the naked eye (Madigan et al., 2015). Bacteria are incredibly abundant throughout the world and represent many species. There are estimated to be at least 1.4 million bacterial species on Earth (Schloss et al., 2016).

Many benefits to the environment are achieved by having a diversity of microorganisms in various places. For example, some microorganisms help clean up pollution by breaking down organics or transforming toxic metals and other chemicals (Madigan et al., 2015). Some microorganisms, such as nitrogen-fixing microorganisms, promote plant growth, and many, including fungi, increase root expansion so that plants can thrive (Taiz and Zeiger 2010). There are also some microorganisms such as pathogenic bacteria and viruses that can cause detrimental results, limiting plant growth or can lead to plant death (Reavy et al., 2014). Even though much is known about many microorganisms, there is still a large number of microorganisms that have yet to be discovered and studied (Madigan et al., 2015). One endeavor that is being used to describe newly discovered microorganisms, as well as macro-organisms is what is known as the All Taxa Biodiversity Inventory (ATBI).

There are arguably millions of species in Great Smoky Mountains National Park (GSMNP) and the ATBI is an attempt to catalog many of the species, including microorganisms, that can be found in GSMNP. According to the ATBI website, there are estimated to be around 100,000 species in GSMNP alone; while this number includes fungi, it likely does not take into account many microscopic species found within the park (ATBI, 2016). As of April 2016, over 9,000 species had been documented in GSMNP, 970 of which are new to science. Of these 9,000 documented species, roughly 500 of them are bacteria (ATBI, 2016). A general hypothesis is that different conditions, for example soil versus water, and many other factors including plant cover type, nutrient chemistry in different environments, as well as elevation and season, etc., may select for different microorganisms, many of which would be new to science. Western Carolina University has an ongoing research project investigating the microorganisms found within GSMNP. This study allows us to obtain more knowledge about the microorganisms in the park and what they may be doing in their environment and to understand any implications. Although, not all bacterial species in a sample can be cultured for a variety of reasons, such as a lack of suitable environment or nutrients for bacterial growth, but ultimately cultivation is required for an acceptable taxonomic record to be made.

Not all bacteria that are identified via molecular testing are also identified with culture testing (Rhoads et al., 2012). Without cultivation in the laboratory, one cannot determine the various metabolic pathways, roles within the environment, or other physiological traits that the isolate may contain by simply looking at the sequence data (Stewart, 2012). In the situation of a novel or understudied species, the DNA sequence may identify species that are closely related, but without the understanding of the physiological and phenotypic traits, the information would be inadequate for a taxonomic record.

The purpose of this project was to characterize and identify a novel species of bacteria from the soil from the Kephart Prong area of GSMNP that can be both sequenced and cultured to provide a full taxonomic record. Previous work had shown that the species was in the genus *Paenibacillus* based on 16S rDNA analyses. This genus is in the phylum Firmicutes, class Bacilli, order Bacillales and family Paenibacillaceae. As of 2012, there have been more than 130 species and 4 subspecies of *Paenibacillus* that have been documented and researched (Mishra et al., 2012). Within GSMNP, there have only been 17 species of *Paenibacillus* found thus far, out of over 1770 total records of bacteria (S. O’Connell, personal communication). *Paenibacillus* species share characteristics most closely related to those of *Bacillus subtilis*, which was first isolated in 1872. Before the division of *Bacillus* and *Paenibacillus*, any bacterium that had the three main characteristics of being “rod-shaped, aerobic or facultatively anaerobic, and could form endospores” were grouped in the genus *Bacillus* (Grady et al., 2016). In 1993, phylogenetic analysis of many 16S rRNA sequences originally classified as *Bacillus* resulted in groupings of new genera, one of which is now defined as *Paenibacillus* (Grady et al., 2016). This genus houses certain endospore-forming bacteria that differ from species of *Bacillus* (Vos et al., 2009) in some of the following ways: being motile via peritrichous flagella, Gram-positive, Gram-negative, Gram-variable, and non-pigmented on nutrient agar (Grady et al., 2016).

The genus *Paenibacillus* contains Gram positive and Gram negative (commonly in older cultures), rod-shaped cells that are either facultatively anaerobic or obligatory aerobic, typically form small, translucent light brown or white colonies and form endospores. These cells usually range from 0.5-0.8µm in width x 2-5 µm in length (Vos et al., 2009). The composition of fatty acids can be diagnostic within the *Paenibacillus* genus and the predominant fatty acid component is C15:0 anteiso, which comprises over half of the cell membrane lipids (Vos et al.,

2009). Some *Paenibacillus* strains are known to be motile and will migrate across agar plates with the help of their peritrichous flagella. In a general sense, the optimum growth parameters for the genus occur in the following ranges: 28-40°C, pH of 7 (but will grow at more alkaline conditions), and NaCl concentrations lower than 10% (Vos et al., 2009). Addition of a fermentable carbon source, such as glucose, to media using these optimum parameters can enhance the growth of *Paenibacillus*.

*Paenibacillus* species are typically found in soil environments rich with plant material and they can hydrolyze a variety of carbohydrates, which include cellulose, starch, and xylan to name a few (Dsouza et al., 2014). Endospores are produced by species within the genus and are one way a species may survive harsh environmental changes, especially nutrient deprivation. Both *Bacillus* and *Paenibacillus* spp. can be found in soil and may be involved in nitrogen fixation and in other ways benefitting the growth of plants, such as in the case of the species *P. polymyxa* (Godvindasamy, 2010). Some strains of *P. polymyxa* are involved in nitrogen fixation and have the ability to suppress plant pathogens (Timmusk and Wagner 1999). *Paenibacillus* species can produce compounds that can suppress fungal diseases as well as antimicrobial compounds that can be utilized in the medical field. The genus *Paenibacillus* houses an assortment of species with a variety of functions of ecological importance. This research project aims to better understand a novel *Paenibacillus* species and its role, whether it be of ecological or of human importance, or both.

### 3. MATERIALS AND METHODS

#### 3.1 Sample Collection

Samples were collected in GSMNP at Kephart Prong (GPS coordinates: N35.35.222 W83.21.431). My sample was taken from the soil using aseptic methods as follows: the top layer of soil was scraped off, then using a heat-sterilized shovel, I removed a soil subsample and placed the sample in a sterile plastic 50-mL centrifuge tube which was placed on ice. The sample was stored at 4°C for 5 days until culture work could begin (O'Connell et al., 2007).

The sample of soil was diluted using a 1:10 series dilution in sterile saline solution. A 100 µL sample from each tube was plated on R2A media and incubated for two days at 25°C. Three colonies were chosen from the 10<sup>-3</sup> and 10<sup>-4</sup> dilution plates and streaked onto three new R2A media plates, then incubated at room temperature. These colonies were re-streaked onto new R2A media plates numerous times, twice a week over a 3- to 4-week span until single isolated colonies were obtained. Due to limited amount of growth on R2A, the isolate was tested for growth on trypticase soy agar (TSA) with 0.7% yeast extract. One selected isolate was then maintained on TSA plates that contained 0.7% yeast extract. This culture showed a high DNA homology to *Paenibacillus* spp. based on 16S rDNA.

#### 3.2 Growth Condition Testing

Once an isolate was obtained, it was tested in triplicate on TSA media under various conditions including: pH of 3, 5, 7 and 9; NaCl concentrations of 1%, 3%, 5%, 7% and 10%; temperatures of 4°C, 25°C, 30°C, 37°C and 50°C; and a control with a pH of 7, 25°C, and 0% NaCl concentration. The presumptive *Paenibacillus* isolate was also inoculated into three separate EnteroPluri™ tubes (Becton, Dickinson, and Company) to determine if it would metabolize glucose, adonitol, lactose, arabinose, sorbitol, and dulcitol by fermentation, lysine by



deamination, and to test whether the isolate would undergo ornithine decarboxylation, sulfur reduction, indole production, acetoin production from glucose fermentation, phenylalanine deamination, urea hydrolysis, and citrate utilization. The isolate was tested for the presence of catalase using a few drops of hydrogen peroxide placed on top of colonies to see if any oxygen gas bubbles were released. The isolate was tested to determine if it contained the respiratory enzyme cytochrome C oxidase by streaking it onto a BBL DrySlide™ (Becton, Dickinson, and Company) and observing the slides for 20 seconds for a color change indicating a positive response. A motility test was also conducted using motility test medium with 0.5 grams/liter triphenyltetrazolium chloride, incubated aerobically at 37°C for 48 hours. A BBL™ GasPack (Becton, Dickinson, and Company) was used to determine if the isolate would grow under anaerobic conditions. The isolate was Gram stained and also negative stained with nigrosin to determine cell size, and shape. A rhizoid growth pattern of the isolate was tested by using dried out nutrient agar plates. This test was performed to determine if the isolate could grow under restricted nutrient conditions. The dried out nutrient agar plates have less nutrients than that of a newly prepared nutrient agar plate due to the depletion of the broth containing the nutrients. The isolate was inoculated in the center of the dried plate and then incubated at 30°C for 48 hours. All of the above laboratory tests were performed minimally in triplicate to account for any variability of response.

The isolate was also tested for its doubling time. Multiple wells of a 96-well plate were filled with 180 µL of TSB and then 20 µL culture broth was added to each well. This test was performed in triplicate with 8 pseudoreplicates of each. The plate was placed in a spectrophotometer with the wavelength set at 650 nm, then readings were taken every 10 minutes for 24 hours. Absorbance data were averaged for each time point plotted to estimate the

doubling time of the culture. The absorbance data was input into Excel, then each set of pseudoreplicates for one reading were averaged using the average function within Excel. Each averaged replicate point was then plotted on an Excel graph and the slope of the graph was calculated using the formula  $\Delta y/\Delta x$ .

### **3.3 DNA Extraction and Amplification**

DNA was extracted from the isolate using the UltraClean Microbial DNA Isolation Kit (Mo Bio Inc., Solana Beach, CA). Partial gene fragments for the 16S rRNA were targeted using PCR for sequencing and identification purposes. The total reaction consisted of 50uL with the following ingredients: nuclease free water (Promega Corporation, Madison, WI), 1X Master Mix chemistry (Promega Corporation, Madison, WI), 0.25uM each primer (bacteria-specific primers 341F and 907R; 341F primer: 5'-CCTACGGGAGGCAGCAG-3' and 907R primer: 5'-CCGTCAATTCMTTGTGAGTTT-3'), and 1uL DNA template (O'Connell et al., 2007).

A touchdown PCR approach was employed, consisting of 5 minutes of initial denaturation at 94°C, then 30 cycles of denaturation at 94°C for 1 minute, annealing for 1 minute, and extension for 3 minutes at 72°C. The annealing temperature in the first two rounds was at 65°C, followed by one round each at 1°C lower than the previous round, and finally eighteen rounds at 55°C. A final extension for 7 minutes at 72°C was employed and then amplicons were stored at 4 °C prior to being sequenced (O'Connell et al., 2007).

### **3.4 16S rDNA Sequence Analysis**

#### **3.4.1 Partial 16S rDNA Sequence Analysis**

PCR products were confirmed by agarose gel electrophoresis and purified. Sanger sequencing for both forward and reverse sequences was carried out by the Virginia Bioinformatics Institute Core Laboratory (Blacksburg, VA), using the same primers as for the

PCR amplifications. The sequences were screened using FinchTV (Geospiza, Inc.®) software and analyzed using the Classifier and SeqMatch tools in the Ribosomal Database Project (RDP) (Cole et al., 2009) and the National Center for Biotechnology Information (NCBI) Basic Local Alignment Search Tool *blastn* (Altschul et al., 1997). For the RDP SeqMatch analysis, the parameters were set at type strain, isolates, size both, and quality good.

### **3.4.2 Full 16S rDNA Sequence Analysis**

The isolate was also sent to GeneWiz ® Laboratory (South Plainfield, New Jersey) to have the entire 16S rDNA gene sequenced and the RDP was used to place the isolate into the taxonomic framework of that database. The top ten sequence matches were pulled from the RDP for further analysis. The full 16S rDNA sequence was also compared to the sequences of the 17 *Paenibacillus* species previously found within GSMNP to determine the percentage of homologous sequence.

## **3.5 Phenotypic Testing**

The closest sequence match based on the full 16S rDNA, *P. castaneae* was researched for various phenotypic tests to further characterize the isolate. The tests that were performed based on this information included: lipase activity, production of indole, nutrient gelatin hydrolysis, mannitol fermentation, nitrate reduction, endospore staining, hanging drop observation, and flagella staining. An additional test that was performed was antibiotic susceptibility testing. Tests were performed in triplicate.

The lipase test contains spirit blue agar with safflower oil and is used to test for the enzyme lipase, which breaks down lipids. The isolates were streaked onto plates that contained this medium and incubated at 37°C for up to 72 hours. *Staphylococcus aureus* was used as a positive control. The indole test is a medium to determine if the organism converts tryptophan to

indole and pyruvate via tryptophanase. Medium for indole production was placed in a 15-mL conical tube and allowed to solidify, then inoculated by stab approach. This was then incubated at 37°C for up to 48 hours. Kovacs Indole Reagent was then added to each tube and observed for 20 seconds to determine a color change, which would indicate a positive result of the production of the byproduct Indole. *Escherichia coli* was used as a positive control (Leboffe and Pierce 2010).

Nutrient gelatin tests were used to determine if the isolate was able to hydrolyze gelatin. Nutrient gelatin (Hardy Diagnostics™) test tubes were used. Three tubes were inoculated using the stab method and placed in a 30°C incubator for up to 24 hours. *Proteus vulgaris* was used as a positive control. In addition to the positive control, a nutrient gelatin tube that was not inoculated was also included due to the tubes being incubated at a temperature higher than room temperature. This blank tube served as a negative control for the time it took for the nutrient gelatin tubes to solidify after removing them from the incubator (Leboffe and Pierce 2010).

Agar containing phenol red, a pH indicator, was used to test if the organism could ferment mannitol. Fermentation of mannitol will cause a shift in the pH, which will cause the color of the agar to change yellow. The molten agar was placed into a 15-mL conical tube, slanted and allowed to solidify in the slanted position. The tubes were inoculated by stabbing directly to the bottom of the tube, then upon removal of the inoculating needle, the isolate was streaked the entire length of the slanted surface. The tubes were incubated at 37°C for up to 48 hours. *Escherichia coli* was used as a positive control (Leboffe and Pierce 2010).

Nitrate reduction tests were performed using Hardy Diagnostics™ premade tubes. Three tubes were inoculated and incubated at 30°C for up to 2 days. The inner tube was observed for any gas bubbles. Regardless of any bubbles, 5 drops of Nitrate Reagent A were added to each of

the three tubes along with 5 drops of Nitrate Reagent B, then the tubes were shaken gently to mix the reagents and the tubes were observed for 1-2 minutes for a deep red color change, indicating a positive result for the presence of nitrite. If no color change was observed after 2 minutes, approximately 6 mg of Nitrate Reagent C was added to each of the three tubes and observed for 5-10 minutes for a deep red color change, indicating a negative result and the presence of nitrate (i.e., no transformation of nitrate to reduced species of nitrogen had occurred; Leboffe and Pierce 2010).

### **3.6 Microscopy**

Endospore staining was conducted on the isolate for a 12 day old culture. A drop of water was added to a slide, a small amount of the isolate was added to the water to emulsify it and then it was heat fixed to the slide by passing it over a flame. After heat fixing, the slide was placed over a beaker over boiling water and a piece of bibulous paper was placed over the slide. malachite green stain was then added on top of the bibulous paper, keeping it saturated, for a total of five minutes. After five minutes, the slide was rinsed with water and counterstained with safranin for one minute, then rinsed again with water (Leboffe and Pierce 2010).

A hanging drop procedure was performed to determine if the cells were motile. To perform this test a drop of water was placed on a slide coverslip and a small amount of culture was added to the water and mixed. A hanging drop slide with Vaseline® around the perimeter was then placed on top of the coverslip, the slide was inverted and the cells were then observed under 1000x magnification (Leboffe and Pierce 2010).

Flagella staining was performed by placing the isolate in a 1.5mL centrifuge tube containing distilled water. The isolate was emulsified in the water until the solution was slightly cloudy. A drop of the culture solution was added to one end of a slide, then the slide was tilted to

allow the solution to run down the slide; the slide was air dried in this position. Once dry, the slide was covered in mordant stain for 4 minutes, then rinsed off with distilled water. The slide was then covered in silver stain, heated until steam was emitted from the slide and then allowed to sit in the silver stain for 4 minutes and rinsed with distilled water and allowed to air dry. Once the slide was dry, it was observed under 1000x magnification (Presque Isle Cultures, Erie, PA).

The isolate was submitted to Wake Forest School of Medicine for transmission electron microscopy. Kenneth Grant and Jamie Wallen performed the following procedure: a small drop (~10 $\mu$ L) of a liquid isolate sample was placed on top of a copper electron microscope grid and allowed to sit for 1-2 minutes to allow the bacteria to adhere to the grid. Using Whatman™ filter paper, excess liquid was removed from the sample by touching the paper to the liquid until only a thin layer of emulsified liquid remained. Working quickly to ensure that the sample on the grid did not dry out, roughly 10 $\mu$ L of filtered 1% uranyl acetate was placed on the grid and allowed to sit for 1-2 minutes. Whatman™ filter paper was used again to remove the excess liquid on the grid. The electron microscope grid was then loaded on the transmission electron microscope and imaged at 13,000x magnification.

### **3.7 Antibiotic Susceptibility**

Antibiotic testing was performed using agar plates that contained TSA with 0.7% yeast extract and a lawn of culture inoculum. The plate was divided up into three sections and within each, one antibiotic disk was placed in the center. This test was performed in triplicate using the following antibiotics: chloramphenicol (30  $\mu$ g), nitrofurantoin (300  $\mu$ g), nalidixic acid (30  $\mu$ g), tetracycline (30  $\mu$ g), colistin (10  $\mu$ g), penicillin (10 units), and clindamycin (2  $\mu$ g) (VWR, Radnor, PA). The antibiotics tested were selected due to cost and availability.

### **3.8 Phylogenetic Tree Analysis**

Twenty closely related 16S rDNA sequences were aligned with Clustal Omega (<http://www.ebi.ac.uk/Tools/msa/clustalo/>) and saved in Nexus format. Phylogenetic trees were reconstructed by maximum parsimony and maximum likelihood methods using PAUP\* version 4.0b (Swofford 2001) accessed through the CIPRES Science Gateway v. 3.3 (<http://www.phylo.org>). The bacterial species *Bacillus eiseniae* was used as an outgroup. For the parsimony analysis, heuristic searches were completed with addition sequence set at random, 100 replicates, and the branch-swapping algorithm set at tree-bisection-reconnection (TBR). A bootstrap analysis was completed using 1000 replicates to assess support for the clades.

For the maximum likelihood analysis, the best model of nucleotide substitution was first determined using the program FindModel (<http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html>). Heuristic searches were completed in PAUP\* on the CIPRES portal with 10 random taxon additions, TBR branch swapping, number of substitution types as six, and the nucleotide frequency and the shape of the gamma distribution value estimated from the data (corresponding to the GTR+gamma model).

### **3.9 Whole Genome Sequencing**

The isolate was also sent to MR DNA Lab (Molecular Research LP, Shallowater, Texas) for whole genome sequence analysis. The library was prepared using Nextera DNA Sample preparation kit (Illumina) following the manufacturer's user guide. The initial concentration of DNA was evaluated using the Qubit<sup>®</sup> dsDNA HS Assay Kit (Life Technologies). Fifty ng DNA was used to prepare the library. The samples underwent the simultaneous fragmentation and addition of adapter sequences. These adapters are utilized during a limited-cycle (5 cycles) PCR in which unique indices were added to the sample. Following the library preparation, the final concentration of the libraries were measured using the Qubit<sup>®</sup> dsDNA HS Assay Kit (Life

Technologies), and the average library size was determined using the Agilent 2100 Bioanalyzer (Agilent Technologies). The libraries were then pooled in equimolar ratios of 2nM, and 10pM of the library pool was clustered using the cBot (Illumina) and sequenced paired end for 500 cycles using the HiSeq 2500 system (Illumina). The entire genome sequence was input into One Codex ([www.onecodex.com](http://www.onecodex.com)) for comparative analyses. Whole genomes of five other *Paenibacillus* species with the highest similarity to the isolate in this study, were included in the One Codex comparisons. Outlier species, *Bacillus subtilis* and a *Cohnella* species, were also added to these comparisons as they represent species with some genomic similarities to the culture in this study.



## 4. RESULTS

### 4.1 Microscopy and Growth Conditions

The colonies on the TSA plates were round with a white, opaque appearance (Figure 1). When isolated colonies were achieved, the size of the colonies were roughly 2-4 mm in diameter. The isolate was Gram-positive, rod-shaped, (Figure 2) and formed endospores. Transmission electron microscopy revealed cells roughly 0.8 $\mu$ m in diameter x 2.8-3.2 $\mu$ m in length with flagella associated with the cells (Figure 3). The isolate had a doubling time of approximately 80 minutes. TSA media with 0.7% yeast extract showed better growth compared to R2A media. The isolate growth was inhibited at 5% NaCl concentrations and growth occurred at a pH of 7 and 9, but not in acidic conditions. Growth occurred at 25°C and 30°C but did not occur at 4°C or 37°C and the culture showed a facultatively anaerobic response. The hanging drop test showed motile rods, both single and in chains, while the flagella stain showed many flagella associated with the cells (Figure 4).

### 4.2 Metabolic Tests

The catalase test showed a weak positive and the test for oxidase was negative. All three sections of the lipid hydrolysis test revealed positive results. There was a partial positive result for the mannitol test, which appeared yellowish-red. The gelatin, casein, and starch hydrolysis tests revealed positive results in all three replicates. The isolate was also able to reduce nitrate from nitrite. The isolate was positive for glucose fermentation, Voges-Proskauer (acetoin production), urease production, and citrate utilization. The isolate showed negative results for gas production from glucose fermentation, lysine and ornithine decarboxylation, hydrogen sulfide production, indole production, adonitol fermentation, lactose fermentation, arabinose fermentation, dulcitol fermentation, and phenylalanine deamination. Results of the performed

metabolic tests for the isolate can be found in (Table 2). The isolate shows little similarities based on the metabolic tests to closely related *Paenibacillus* species from 16S rDNA and whole genome analysis (Table 2).

#### **4.3 Antibiotic Susceptibility**

Antibiotic testing revealed visible clearings around five of the antibiotics, one slight inhibition ring around penicillin and no inhibition around colistin, indicating that the isolate is resistant to colistin, but susceptible to all other antibiotics tested (Figure 5).

#### **4.4 Phylogenetic Tree Analysis**

Based on the top 20 most homologous 16S rDNA sequences to that of the isolate retrieved from the RDP database, the isolate was most closely related to the species *Paenibacillus pinisoli* and *Paenibacillus nanensis* (Figure 7a). A bootstrap method was performed on the parsimony tree using the top 20 most homologous 16S rDNA sequences to the isolate, and out of the 100, the clade containing *P. pinisoli* and *P. nanensis* only occurred 53 (or 53%) times. The cut-off value for this tree was 50 (or 50%) and the clade containing the isolate being tested did not have a percentage, hence this clade occurred less than 50% of the time (Figure 7b) and does not show a high level of support for this clade. These phylogenetic trees were verified using a maximum likelihood and strict consensus methods. After the top 20 most similar sequences of *P. pinisoli* and *P. nanensis* were added to the phylogeny, the maximum likelihood analysis revealed that the isolate species was more closely related to *P. pinisoli* (Figure 7c). The strict consensus analysis of the two most parsimonious phylogenetic trees also showed that the isolate is more closely related to *P. pinisoli* (Figure 7d).

#### **4.5 16S rDNA Sequence Analysis**

The full 16S rDNA sequence was input into the RDP tool Classifier, and the taxonomy indicated a 100% confidence at each level from the Domain *Bacteria*, phylum Firmicutes, class Bacilli, order Bacillales, family Paenibacillaceae, and genus *Paenibacillus*. The RDP program SeqMatch found that the highest sequence match in the RDP database was *Paenibacillus castaneae* with an 84.6% similarity and the next highest match was *Paenibacillus agaridevorans* with an 84% sequence similarity (Table 1).

When the full 16S rDNA sequence was compared to the sequences of the 17 different *Paenibacillus* species found within GSMNP, no species for a previously detected *Paenibacillus* was greater than 95% sequence homology. The closest sequence matches to the isolate out of the species found within the park were *P. xinjiangensis*, *P. terrigena*, and *P. pabuli*, all with a 95% sequence homology.

#### **4.6 Whole Genome Sequence Analysis**

MR DNA returned a likely partial genome of 14 contiguous sequences (contigs) ranging in size from 5,068 to 1,532,455 bp. An overview of information from the genome can be found in Table 3, including the genome size of 5,281,746 bp, 4,955 putative genes, and a G+C content of 41%. All 20 tRNA sequences were found within the genomic sequence, which indicates that even though there may be gaps within the genome, it is largely complete. Roughly 4,900 putative genes were proposed using Illumina's BaseSpace tools and some genes of interest can be found listed in Table 5, including antibiotic and multi-drug resistance, chitinase, sporulation, and flagella genes. One Codex showed a high genomic homology of the isolate in this study to *Paenibacillus harenae* (genome size of approximately 6.9 Mb) and the closest genome size to the isolate is *P. polymyxa* (genome size of approximately 5.8 Mb). For *P. polymyxa*, 11 of the 14 contiguous sequences revealed matches ranging from 77% to 98% sequence similarity using

NCBI BLAST® alignment for this latter species compared to the isolate. Overall, OneCodex revealed that the isolate did not match known genome sequences for any *Paenibacillus* spp. (Figure 6a and 6b). At the genus level, the isolate appears to include genome sequences from *Brevibacillus*, while at the species level of analysis, the isolate appears to incorporate multiple DNA sequences from other *Paenibacillus* species as well as from *Bacillus* and *Cohnella* species.

## 5. DISCUSSION

Parameter testing, analysis of the full 16S rDNA sequence, and the whole genome sequence suggest that a novel species has been discovered. Results from these methods suggest that the novel species might be within the genus *Paenibacillus*, or is closely related to this genus. The highest sequence match in RDP was 84.6%, to *P. castaneae*, much lower than the conventional cutoff for species of 97%. Therefore, it can be assumed that this isolate is a novel species, but possibly in the same genus, according to the RDP Classifier results.

Metabolic testing supports the assumption that this is a novel species because the results of the isolates metabolic test show little similarities to the closely related *Paenibacillus* species from the 16S rDNA analysis. The species that the isolate has the most similarities to based on metabolic tests is *P. polymyxa* (Table 2). Even though the isolate's metabolic test results most resembles that of *P. polymyxa*, the 16S rDNA and whole genome sequences differ substantially to that of *P. polymyxa*; therefore, there is a highly likelihood that this isolate is not *P. polymyxa* and is not the species that are most closely related based on the 16S rDNA and genomic sequence analysis.

When the genomic sequence was analyzed using OneCodex, it revealed the possible origins of some DNA from other species (Figures 6a and 6b). A larger portion had a match to *P. harenae* with other smaller sections revealing matches to *Brevibacillus laterosporus*, *P. odorifer*, *P. assamensis*, and *P. pini*. This result could indicate the uniqueness of the isolate sequence, perhaps via horizontal gene transfer, as other *Paenibacillus* genomes appeared to be comprised of DNA from a single taxon.

Genomic sequence analysis by MR DNA revealed that the isolate has a genome size of roughly 5.3 Mb and a G+C content of about 41% (Table 3). Based on the G+C content value, the

isolate can be found within the genus *Paenibacillus*, which has a G+C content range of 40-59% (Vos et al., 2009). With all of the 20 different tRNA genes found within the genome sequence, it can be assumed that at least 90% of the genome sequence has been retrieved through this analysis. Of the 4,955 putative genes retrieved from the genomic sequence analysis, 3,637 of them had a predicted gene function ranging from resistance genes to movement and development genes (Tables 2 and 3).

Genes found within the genomic sequence revealed how the isolate can survive within its environment, how it moves, how it is able to receive energy, and other functions. Sporulation, and antibiotic resistance genes might allow the isolate to respond under stressful conditions. By producing spores, the isolate would likely survive periods of nutrient scarcity or other adverse conditions (low temperature, desiccation, etc.; Nicholson et al., 2000). Antibiotic resistance provides many bacteria with the ability to pump out chemicals that threatens the integrity of the cell or by restricting the uptake or inactivating the antibiotic (Lambert, 2002). Some antibiotics can be found naturally occurring and are developed from various strains of bacteria and fungi; at least two-thirds of antibiotics that are found within soil are produced by actinomycetes (Fair and Tor 2014). This isolate would likely be subject to exposure to antibiotics in nature, so having the ability to protect itself from them is crucial. In the antibiotics that were tested, only one was ineffective against the isolate.

A number of bacitracin resistance genes were found within the genome sequence. These genes are important for the isolate because bacitracin targets Gram positive bacteria and it disrupts the production of the peptidoglycan of the cell walls (Mascher, T. et al., 2003). Although the isolate was not tested against bacitracin, an antibiotic that also inhibits synthesis of peptidoglycan was tested, which was penicillin (Yocum et al., 1980). Penicillin did not reveal a

strong inhibition around the disk, but since there was a small inhibition ring, the isolate may be resistant up to a certain concentration. Susceptibility at 30 µg/disk was tested, but a lower dose may reveal complete resistance. The response to penicillin may indicate how the isolate would respond to bacitracin; the isolate may be resistant to this antibiotic up to a certain concentration. Another antibiotic resistance gene found within the genome coded for tetracycline resistance, but during the antibiotic resistance testing, the isolate was susceptible to tetracycline. Once again, this could potentially be explained by the concentrations of tetracycline. Susceptibility at 30 µg/disk was tested, but perhaps a lower dose or in a different medium would have produced different results.

Other antibiotics were tested against the isolate for susceptibility in the absence of resistance genes being seen within the genome sequence. Nalidixic acid is an antimicrobial agent that is effective by inhibiting the replication of DNA. This antibiotic achieves this by inhibiting the activity of DNA gyrase, an enzyme that bacteria use to negatively supercoil double-stranded DNA into closed circular DNA during the replication process (Gellert et al., 1977). In addition clindamycin and chloramphenicol were also tested; these antibiotics inhibit bacterial protein biosynthesis (Kehrenberg et al., 2005). Protein biosynthesis is part of the translation process and when this is inhibited, it will inhibit the growth of new cells (Laursen et al., 2005).

Nitrofurantoin is involved in the inhibition of enzyme synthesis involved in metabolism of carbohydrates and the synthesis of the cell wall (Munoz-Davila, 2014). Finally, colistin is an antibiotic that targets primarily Gram-negative bacteria that is assumed to have the same mechanism of action as polymyxin B due to its amino acid makeup. Polymyxin B alters the lipid makeup of the cell membrane (Nation and Li 2010). Even though this isolate did not contain resistance genes for colistin, having them could be beneficial for when older cultures have cell

wall structures that are damaged or weakened. In older cultures of *Paenibacillus*, the cell wall can exhibit Gram-negative characteristics, potentially from the breakdown of the cell wall composition.

Some of the genes within the genome sequence may involve means of acquiring energy or nutrients through a variety of methods. The isolate has the ability to break down blood cells based on lab and gene sequencing results and the genome suggest that it could use heme, perhaps as an iron source. In addition to this, the isolate had a large number of genes that were involved in siderophore production. Siderophores are excreted from bacterial cells and bind to various metals, including iron, which are commonly found within soil and water environments. Once the metals are chelated by siderophores, bacteria and plants can uptake the bound metals and use them in metabolism (Ahmed and Homström 2014).

Mobile element genes were found within the genomic sequence. Mobile elements can be utilized by bacteria to horizontally or laterally transfer genes within the bacterial chromosome and can lead to antibiotic resistance and plasticity, or the ability to adapt to environmental changes. These types of changes are induced by the presence of various environmental changes (e.g. temperature changes, etc.) and by the exposure of antibiotics (Malachowa and DeLeo 2010). Plasmids play an important role in horizontal gene transfer (HGT) by allowing the transfer of DNA to related bacteria. This mechanism also aids in the transfer of antibiotic resistance genes. Transformation, transduction, and conjugation are the three methods in which bacterial DNA can be transferred with the assistance of plasmids. Many of the resistance plasmids are conjugative plasmids, which contains the DNA required for cell-to-cell coupling. The cell-to-cell coupling requires a pilus structure to attach the cells, allowing for envelope contact, then development of pores for DNA transfer (Bennett, 2008).



Type IV pilus genes can play a role in the recombination of DNA, as well as in other functions including motility, phage attachment, cell signaling, etc. These genes can also play a role in pathogenicity, but more analysis of the genes in this isolate would have to be conducted to determine the structure of the pilus gene products; structure is the main indicator of the role that the pilus plays within the isolate (Craig et al., 2004). The isolate may have some role in pathogenicity due to the pilus genes plus an adhesin gene, which would be needed in pathogenic bacteria to bind to the host cells (Klemm and Schembri, 2000). Based on the putative genes that were found within the genome, the isolate may have potential to be a pathogen, but without further analysis of the pilus structure, it cannot be definitively concluded that the isolate is a pathogen.

The size of genomes within the Paenibacillaceae family ranges from 3.83Mb to about 8.9Mb with the mean size being about 6.05Mb. Some of the species within this family that have genome sizes of 3.5Mb to about 5Mb are known to be insect pathogens and are fastidious, which makes it difficult to keep them growing within the laboratory (Zeigler, 2013). The genome size of the isolate being studied is about 5.2Mb, which is slightly larger than those known to be found within the insect pathogen range, but it could give insight as to why this isolate doesn't grow well on particular media, such as R2A, which is nutrient limiting. According to Zeigler, out of the genomes that have been sequenced within the Paenibacillaceae family, one of the closest matches to the genome size of the isolate is *P. polymyxa*. When the whole genome of *P. polymyxa* was compared to the genome of the isolate, 11 of the 14 contiguous sequences returned matches but not with high homologies.

*P. polymyxa* is well known for its benefit in the environment, primarily promoting plant growth and suppressing plant disease. A few things that *P. polymyxa* is capable of is nitrogen-

fixation, plant hormone production (Weselowski et al., 2016), and antimicrobial activity by producing polymyxins that target Gram negative bacteria (Velkov et al., 2013) all of which can be beneficial in its role of promoting plant growth (Weselowski et al., 2016). In comparison to the isolate being studied, both species can be found within the soil. In regards to colony appearance and growth parameters, both species appear a white-cream color on TSA media, both are able to hydrolyze gelatin, and both species revealed a weak positive in the acid formation within the mannitol test. Although there are similarities between the two species, there are differences as well. One major difference is that *P. polymyxa* is able to grow at a temperature of 40°C but the isolate in this study could not.

*P. pinisoli* was compared to the isolate being studied because of the phylogenetic tree analyses. This species of *Paenibacillus* has also been discovered within soil environments (Moon and Kim 2014). With the full 16S rDNA sequence analysis comparison to *P. pinisoli*, there was only an 83.7% sequence homology, well under the 97% cut-off. In addition to sequence analysis, growth conditions were compared, which revealed that only three of the tested conditions of *P. pinisoli* matched to that of the isolate. Whole genome sequence comparison of *P. pinisoli* and the isolate being tested could not be performed due to no genome sequence of *P. pinisoli* being documented thus far.

The isolate in this study is related to, but distinct from *P. polymyxa*, *P. nanensis*, *P. castaneae*, *P. agaridevorans*, and *P. pinisoli* and therefore it can be said the isolate being studied can be proposed as a novel species. The species *P. polymyxa* was chosen for comparative analysis due to the size of the genome being the closest to that of the isolate being studied. Though the 16S rDNA sequences of the isolate was most closely related to *P. castaneae* and *P. agaridevorans*, the results of the growth condition tests were significantly different and the G+C

content of the isolate genome was unlike, especially in *P. agaridevorans* with a 9-11% difference. This information can be further supported by the growth conditions testing comparisons of the isolate to these species found in Table 2. In addition to the differences in growth conditions and 16S rDNA sequences, there is a substantial difference in the 16S rDNA phylogenetics to warrant designation as a new species. This is further supported by information from the whole genome sequence analyses.

## 6. CONCLUSION

Within GSMNP, there have been relatively few *Paenibacillus* species discovered from the various sampling areas within the park. With the discovery of this species, it can inform GSMNP personnel in the understanding of the bacterial diversity within the park. In addition to the Park inventory, this information can aid in the understanding of the diversity within the genus *Paenibacillus*. This diversity could provide information in the evolving bacterial species and give insight to what this species does within its environment. As in the case of *P. polymyxa*, it may produce some antimicrobial or plant hormone benefits, but could also potentially have pathogenic potential, both instances could have ecological and clinical importance. Once the species has been classified and the ecological role is better established, the 16S rDNA and whole genome sequence can be used to uncover this species within different regions within the Park and throughout the world to recognize various environments that it can be found.

Even with the discovery of the novel *Paenibacillus* species, there is still a lot to learn about what this species may do within the environment and with other organisms. To assist in the determination of the role of this bacterium within the environment, the entire genome sequence will need to be sequenced to fill in the gaps between contiguous sequences. Once the whole genome sequence has been constructed, it can be compared to other species to determine a more taxonomic placement, and it can also provide insight into more functions that may exist in the bacterium. In addition to the sequence analysis, once whole genomes of the most closely related species become available, whole genome phylogenetic trees can be constructed; this will provide another more precise sequence comparison. Other tests that can be performed include chitinase tests to determine if the bacteria utilizes chitin as suggested by its genome. To determine whether this species is a pathogen, the pilus structure can be further analyzed. If this species is in fact a

pathogen, it can then be compared to that of other pathogenic species within the *Paenibacillus* genus. A new bacterial species has been discovered in Great Smoky Mountains National Park and will be added to the ATBI. This work showed a possible ecological role of the bacterium in soil, including the use of a suite of carbon sources as well as metabolism of other materials. Future work will challenge the bacterium with additional phenotypic testing and searches for genes of known and unknown function and testing them to learn more about the biology of this organism. From a global perspective, another species of bacteria has been informally classified and future work will involve taking the necessary steps to classify this new species.

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## 8. TABLES

Table 1. Sequence Similarities for the full 16S rDNA sequences of the isolate in this study compared to species included in the RDP database.

Species	Percent Similarity
<i>Paenibacillus castaneae</i>	84.6%
<i>Paenibacillus agaridevorans</i>	84.0%
<i>Paenibacillus pinisoli</i>	83.7%
<i>Paenibacillus nanensis</i>	83.5%
<i>Paenibacillus endophyticus</i>	83.1%
<i>Paenibacillus quercus</i>	82.5%
<i>Paenibacillus prosopidis</i>	82.2%
<i>Paenibacillus agarexedens</i>	82.2%
<i>Paenibacillus alkaliterrae</i>	81.9%
<i>Paenibacillus harenae</i>	81.6%

Table 2. Some phenotypic and other characteristics of the isolate in this study in comparison to other *Paenibacillus* species (information for other species adapted from Valverde et al. 2008, Vos et al. 2009, and Moon and Kim 2014). nd = not determined.

	Isolate	<i>P. polymyxa</i>	<i>P. assamensis</i>	<i>P. graminis</i>	<i>P. odorifer</i>	<i>P. popilliae</i>	<i>P. castaneae</i>	<i>P. agaridevorans</i>	<i>P. pinisoli</i>
<b>Anaerobic Growth</b>	+	+	nd	+	+	+	-	-	-
<b>Catalase</b>	+	+	+	+	+	-	+	+	+
<b>Oxidase</b>	-	-	+	-	-	-	+	+	+
<b>Nitrate Reduction</b>	+	+	-	+	+	-	-	-	nd
<b>Voges-Proskauer</b>	+	+	nd	nd	nd	+	-	-	nd
<b>Casein</b>	+	+	+	nd	nd	-	-	-	nd
<b>Gelatin</b>	+	+	+	nd	nd	-	+	-	nd
<b>Starch</b>	+	+	+	+	+	-	-	-	nd
<b>Urea</b>	+	-	-	+	nd	nd	-	nd	nd
<b>Indole</b>	-	-	-	-	nd	-	-	-	nd
<b>Citrate</b>	+	-	-	nd	nd	-	-	-	nd
<b>Optimal Growth Temperature, °C</b>	30	30	nd	28	28	28-30	30	30	25-40
<b>Growth at 50°C</b>	-	-	-	-	-	-	-	-	-
<b>5% NaCl</b>	-	-	-	nd	nd	-	-	-	+
<b>7% NaCl</b>	-	-	-	nd	nd	-	-	-	-
<b>G+C (mol%)</b>	41	43-46	41.2	52.1	44	41	46	50-52	54.5

\*Indicates a weak positive

Table 3. Summary of whole genome information retrieved from MR DNA approach.

<b>Genome Information</b>	
Genome Size (bp)	5,281,746
G+C content (%)	41
Total tRNA genes	62
16S rRNA genes	8
Different 16S rRNA genes	0
Contigs with 16S rRNA genes	6
Total number of putative genes	4,955
Genes with function prediction (%)	3,637 (73.4%)
Genes without function prediction (%)	1,318 (26.59%)

Table 4. Categories of putative genes from whole genome sequencing including possible functions or roles and how frequently they were found.

<b>Gene</b>	<b>Number of Total Genes</b>
Antibiotic/multi-drug resistance	105
Metal resistance	30
Chitin use	70
Sporulation/Germination	96
Capsule formation	9
Siderophore	30
Heme uptake and use	23
Heme biosynthesis	9
Mobile elements	5
Phage genomes	28
Flagella	53
Type II/IV Pilus	11
Virulence	1

## 9. FIGURES

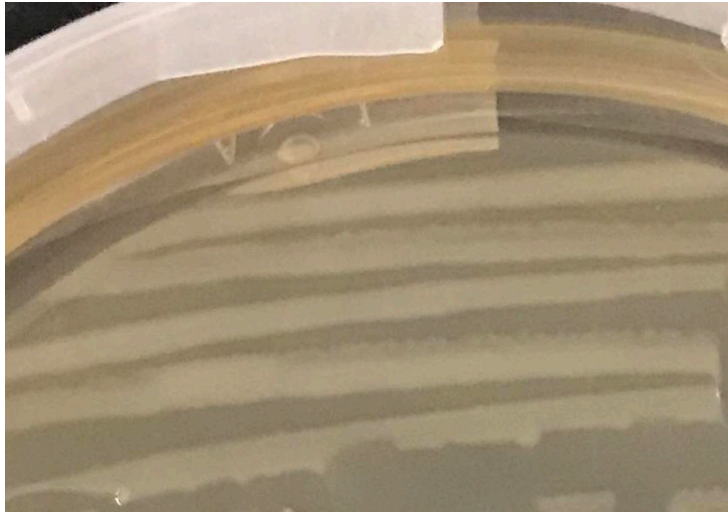


Figure 1. Culture characteristics on TSA media showing the isolate having an opaque white appearance. No viable isolated colonies can be seen.

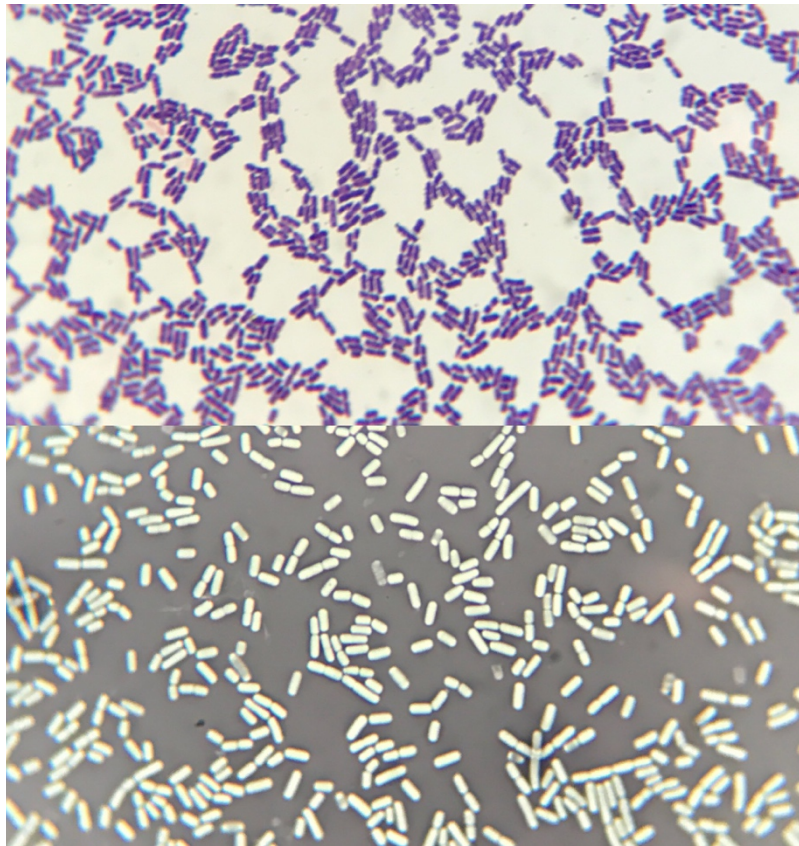


Figure 2. Light microscope image of the isolate revealing a Gram-positive cell wall composition (top) and the negative stain results showing rod-shaped cells (bottom).



Figure 3. Transmission electron micrograph of the isolate (performed by Jamie Wallen and Kenneth Grant at Wake Forest School of Medicine).

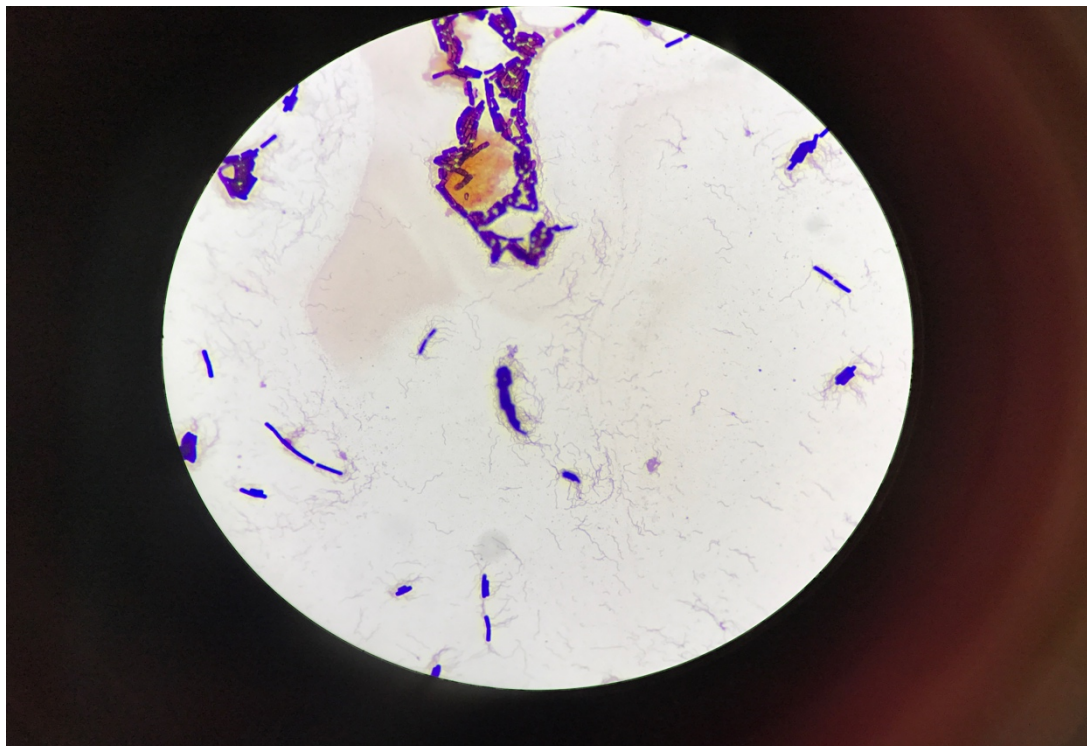




Figure 4. Flagella stain result shown at 1,000x magnification with purple structures, the cells, and flagella are both attached and unattached to the cells.

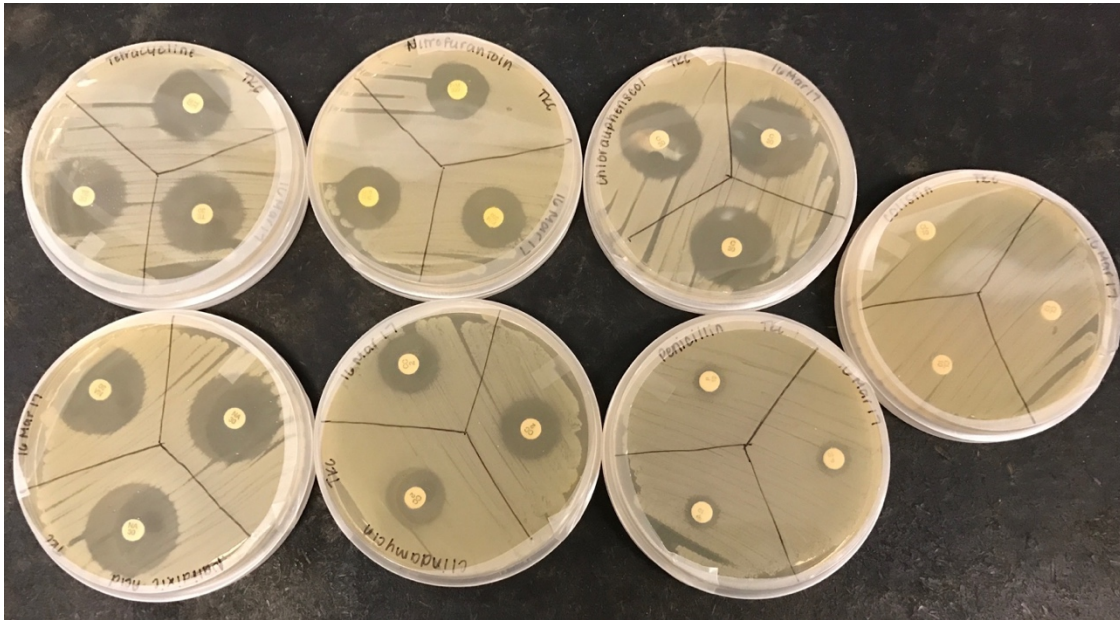


Figure 5. A depiction of the antibiotic susceptibility testing showing five out of the seven antibiotics creating zones of inhibition. Antibiotic listing (clockwise starting at top left): tetracycline, nitrofurantoin, chloramphenicol, colistin, penicillin, clindamycin, and nalidixic acid.

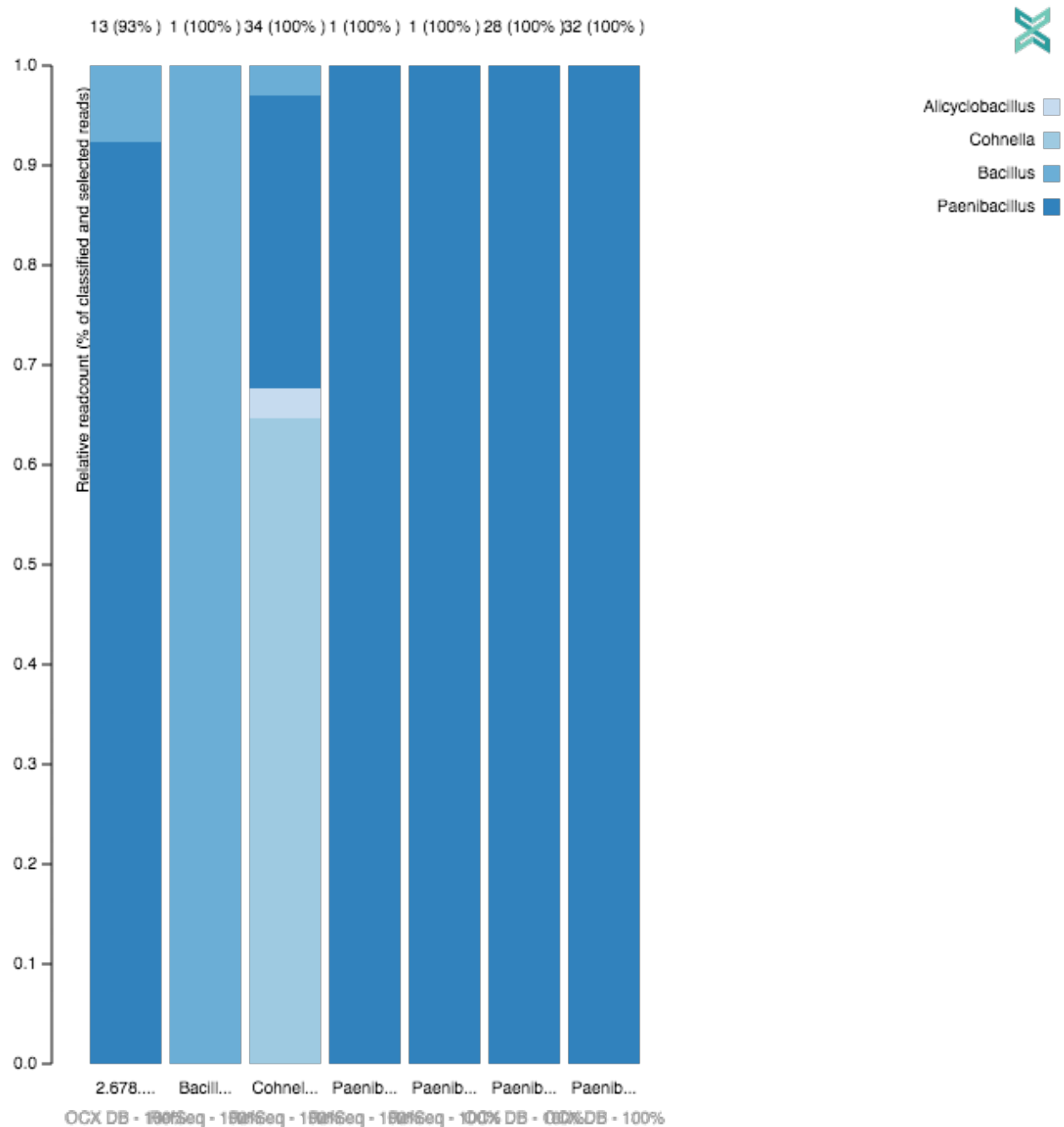


Figure 6a. Results from the OneCodex analysis at the genus level with the addition of both *B. subtilis* and a *Cohnella* spp. Sequences are listed from left to right as follows: Isolate, *Bacillus subtilis*, *Cohnella* spp, *P. odorifer*, *P. graminis*, *P. harenae*, and *P. assamensis*. The strains used for comparison were retrieved from the NCBI Whole Genome sequence database.

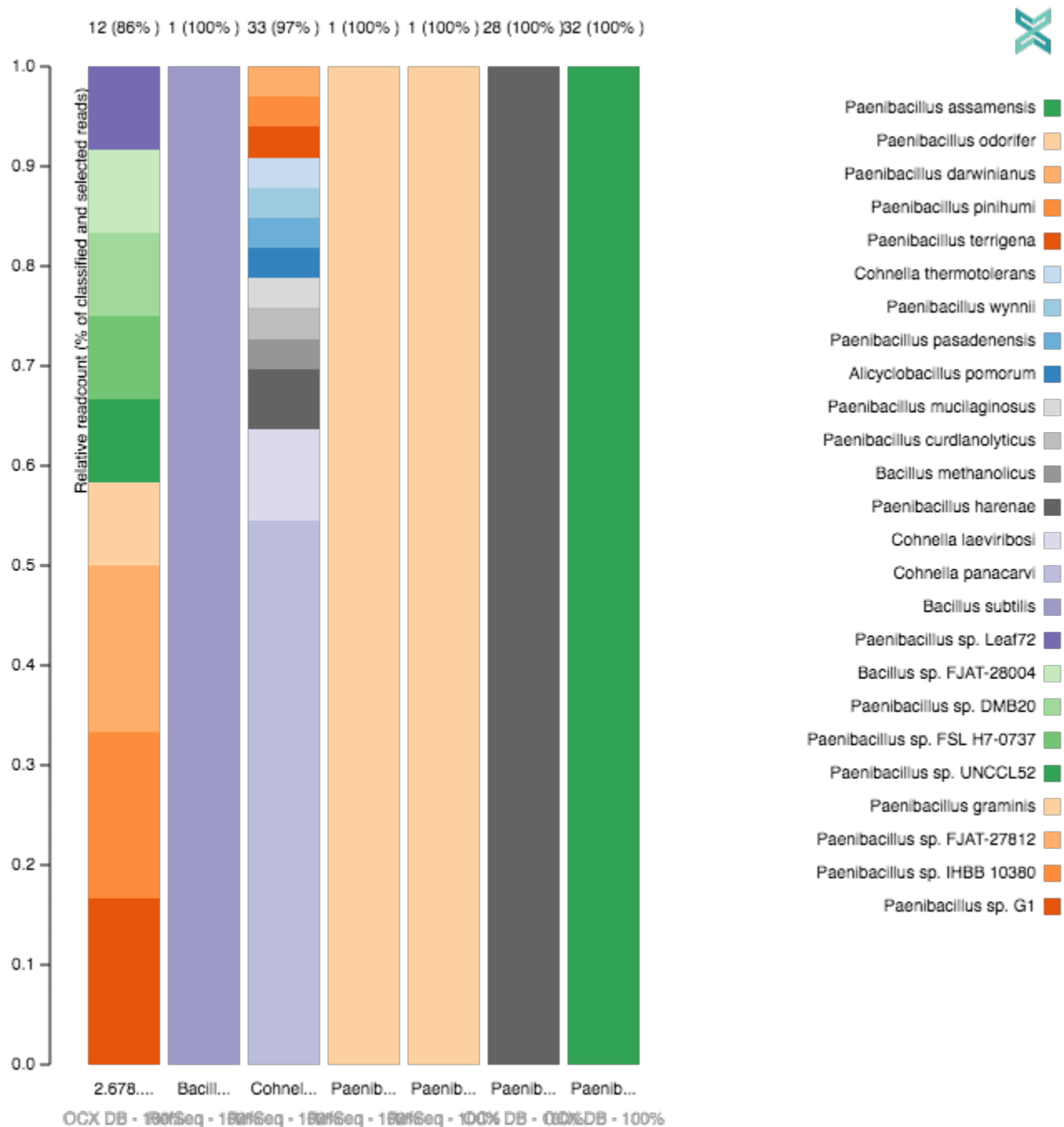


Figure 6b. Results from the OneCodex analysis at the species level with the addition of both *B. subtilis* and a *Cohnella* spp. Sequences are listed from left to right as follows: Isolate, *Bacillus subtilis*, *Cohnella* spp, *P. odorifer*, *P. graminis*, *P. harenae*, and *P. assamensis*. The strains used for comparison were retrieved from the NCBI Whole Genome sequence database.



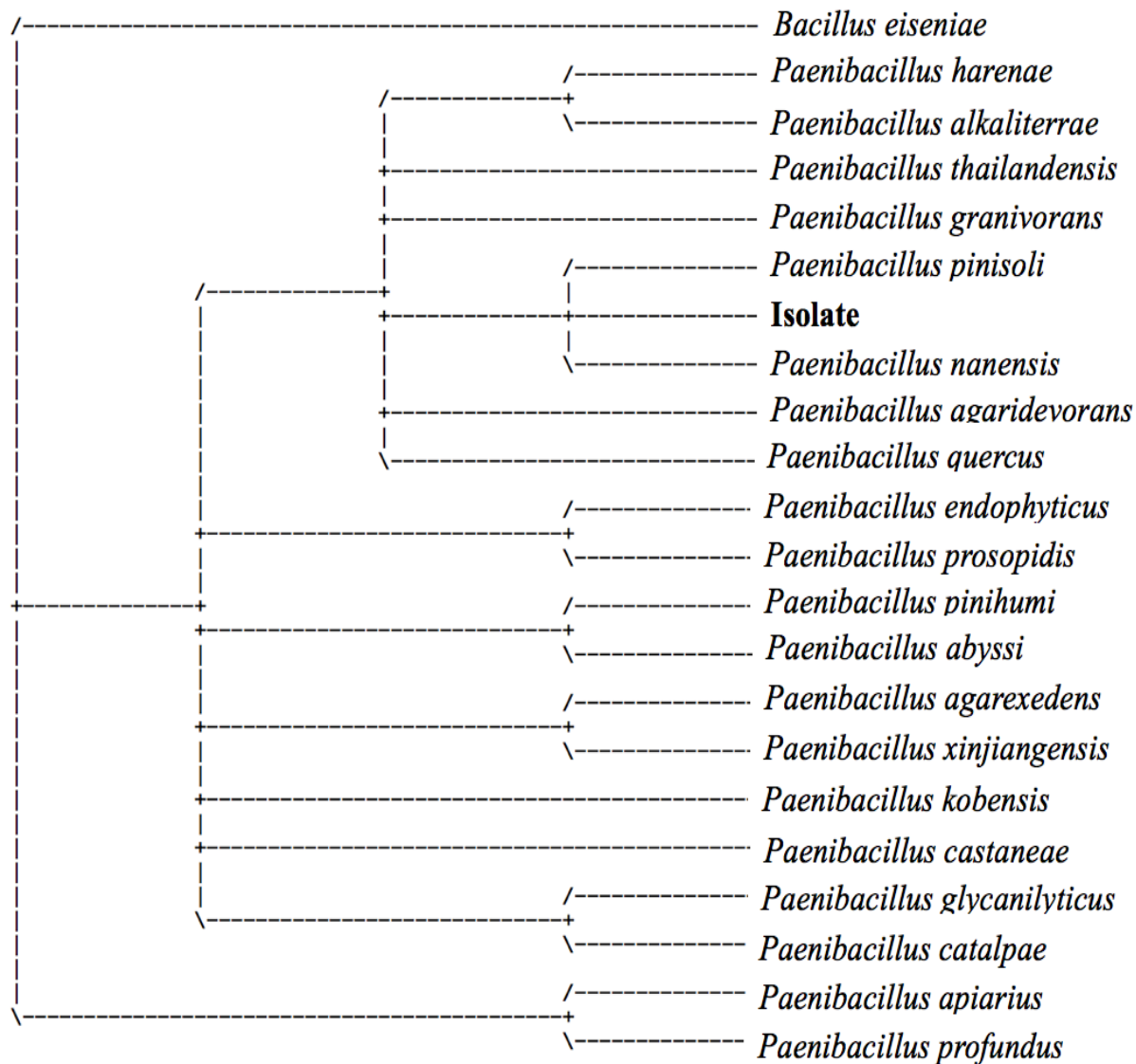


Figure 7a: Parsimony phylogenetic tree analysis of the 16S rDNA sequence of the isolate being studied compared to the top 20 homologous *Paenibacillus* species from the RDP SeqMatch database. *Bacillus eiseniae* serves as the outlier species.

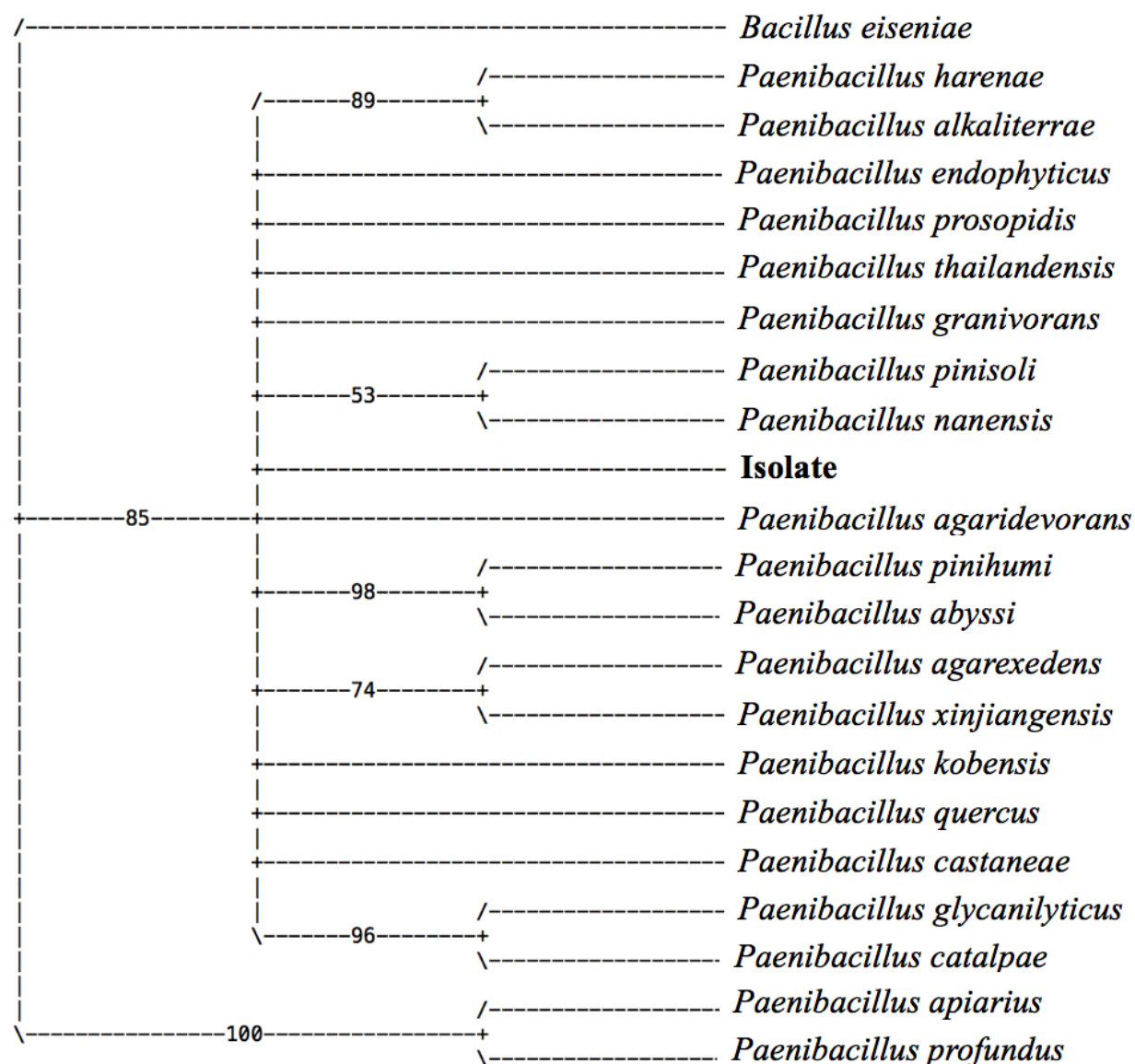


Figure 7b. Bootstrap phylogenetic tree analysis of the 16S rDNA sequence of the isolate being studied compared to the top 20 homologous *Paenibacillus* species from the RDP SeqMatch database. *Bacillus eiseniae* serves as the outlier species. This method analyzed a total of 100 trees with a clade cut-off of 50%.

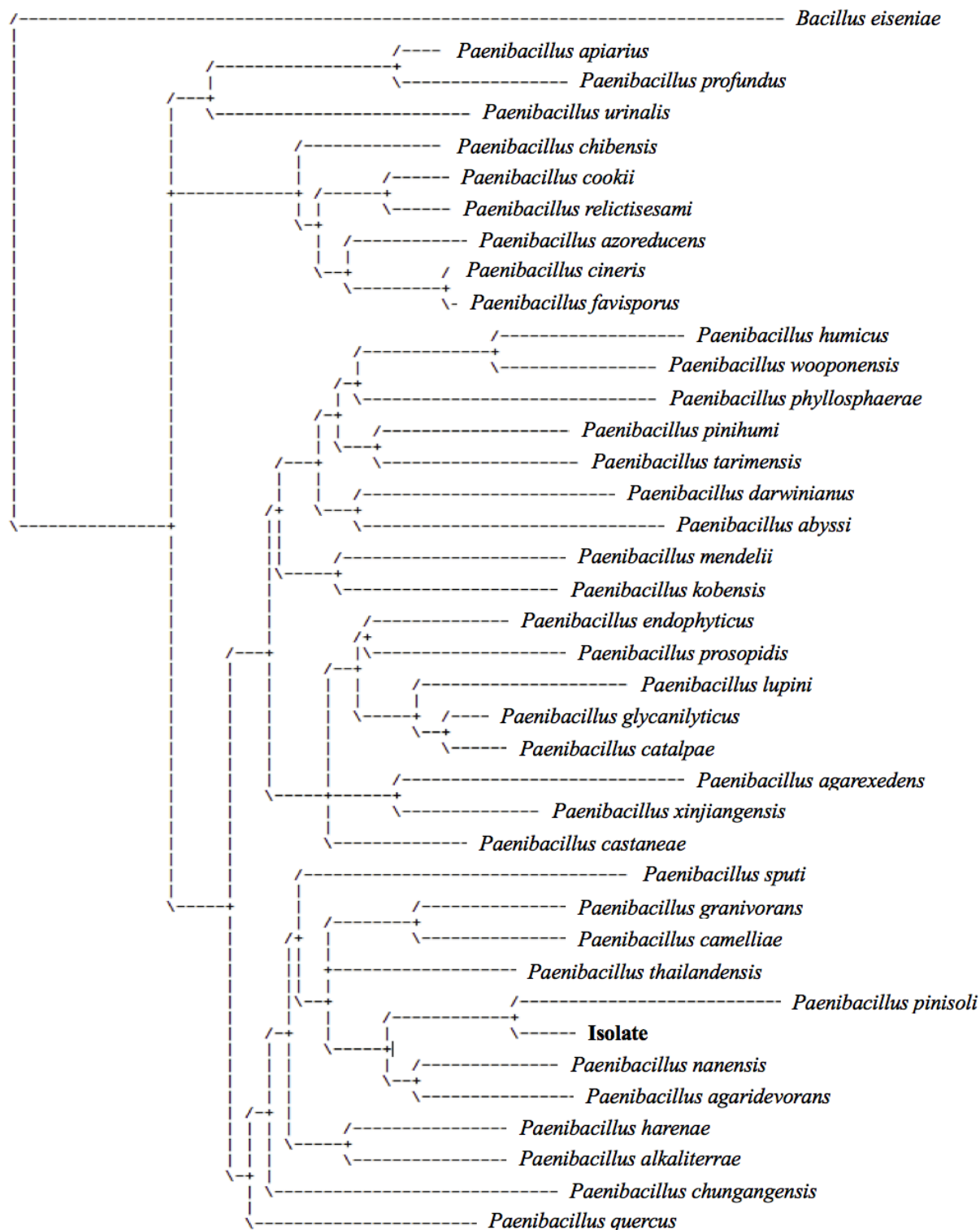


Figure 7c. Maximum likelihood phylogenetic tree analysis of the 16S rDNA sequence of the isolate compared to the top 20 homologous 16S rDNA sequences in the RDP SeqMatch database in addition to the top 20 homologous 16S rDNA sequences to the two most closely related *Paenibacillus* species from the parsimony phylogenetic tree (Figure 7a). *Bacillus eiseniae* serves as the outlier species.

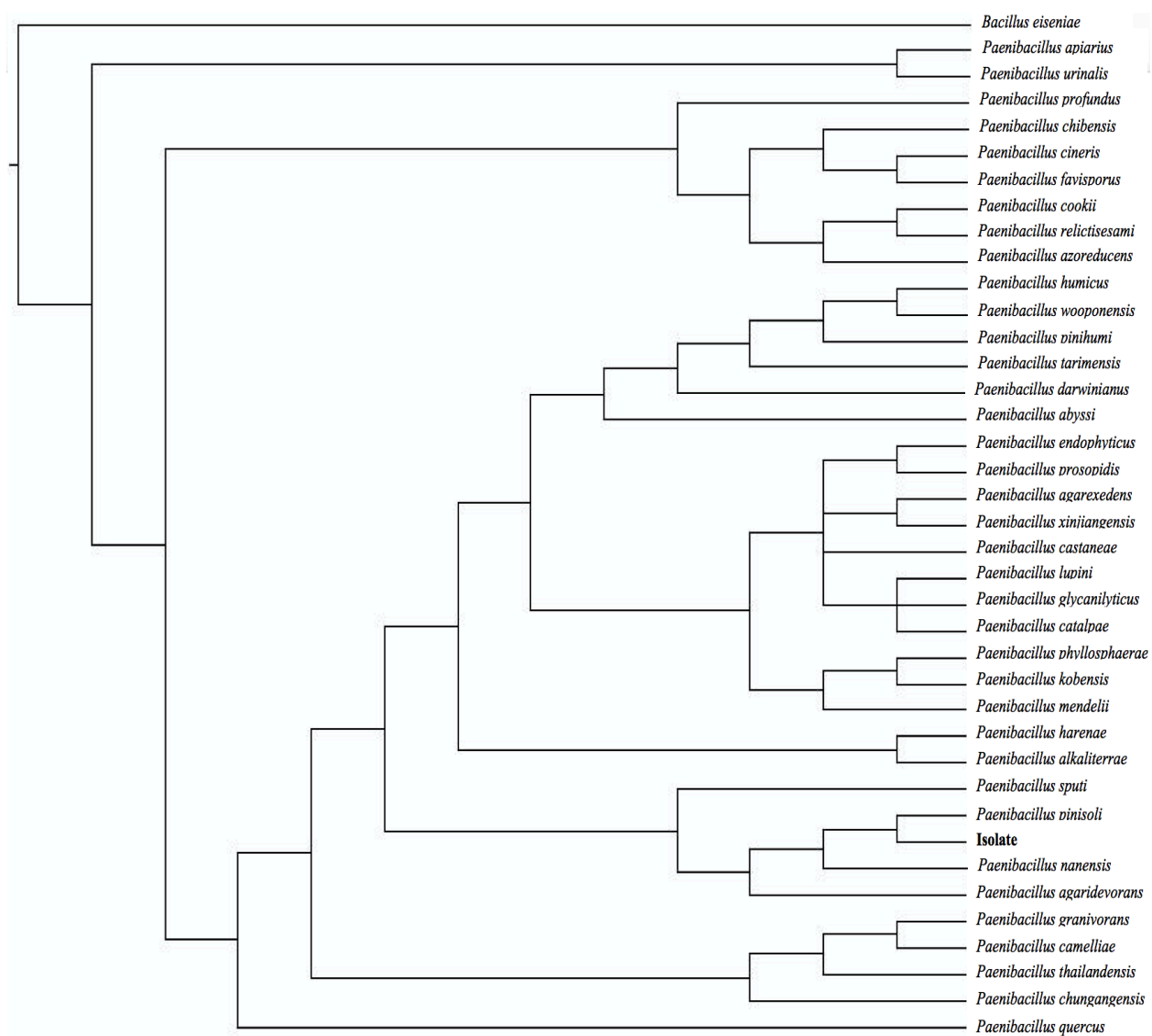


Figure 7d. Strict consensus tree of the two most parsimonious tree analyses based on the most homologous 16S rDNA sequences to that of the isolate.

## 10. APPENDIX

### 10.1 Contiguous Sequences from Genome Sequence Analysis

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at t t c t t t t t c t t t t t c t a g c t c t t c a g c a g a a c c t c t t c a c g a c g a a c  
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